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portions of the fibro-vascular systems may also serve their usual purpose of conductors of water.

EXPLANATION OF PLATES.

PLATE IV.

FIG. 1.—Sketch of a gall showing its ordinary form, size and position. Natural size.

FIG. 2.—Sketch of the gall showing its appearance when found above the first set of leaflets.

FIG. 3.—Several galls on the same petiole showing the effect on stem and the general arrangement and shape of the galls when more than one occurs on the same petiole.

FIG. 4.—Cross section of gall and petiole, showing internal appearance of gall.

PLATE V.

FIG. 5.—Cross sections of normal petiole; *a*, at base, no well-developed second row of fibro-vascular bundles; *b*, below first pair of leaflets, appearance of second row of fibro-vascular bundles; *c*, above first pair of leaflets, a well-developed second row of fibro-vascular bundles. × 25.

FIG. 6.—Clustered hairs. × 165.

FIG. 7.—Glandular hairs. × 165.

FIG. 8.—Gall hairs, extensions of epidermal cells.

PLATE VI.

FIG. 9.—Cross section of petiole and gall; *a*, gall hairs which appear to be continuations of the epidermis *b*; *c*, parenchyma beneath the epidermis; *d*, fibro-vascular bundles in which tracheids have supplied the place of tracheary and other vessels; *e*, parenchyma of the pith (highly magnified).

FIG. 10.—Longitudinal-radial section of petiole and gall; *a*, *b*, *c*, *d*, *e*, as in fig. 9 (highly magnified).

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ON THE EVOLUTION OF THE VERTEBRATA, PROGRESSIVE AND RETROGRESSIVE.

BY E. D. COPE.

I. PRELIMINARY.

IN attempting to ascertain the course of evolution of the Vertebrata, and to construct phylogenetic diagrams which shall express this history, among the difficulties arising from deficient information, one is especially prominent. As is well known, there are many types in all the orders of the Vertebrata which present us with rudimentary organs, as rudimental digits, feet or limbs, rudimental fins, teeth and wings. There is scarcely an organ or part which is not somewhere in a rudimental and more or less useless condition. The difficulty which these cases present is, simply, whether they be persistent primitive conditions, to be regarded as ancestral types which have survived to the present time, or whether, on the other hand, they be results of a process of degeneration, and therefore of comparatively modern origin. The question, in brief, is, whether these creatures presenting these features be primitive ancestors or degenerate descendants.

In the first place let us define the meaning of the word degenerate. This must be done first from a structural or anatomical standpoint. Degeneracy may be defined as a loss of parts without corresponding development of other parts. All animals are degenerate in some respect or another, as, for instance, the Mammalia in the small size of the pineal gland and of the coracoid bone; so that degeneracy, as a whole, can only be affirmed where the sum of the subtractions is greater than the sum of the additions. Function of the parts must, however, be consulted in this matter. We naturally regard sensibility as the highest of animal functions, and mind as the highest form of sensibility. Therefore development of organs of sensibility and sense and mind constitutes a better claim of progress than development of stomach or of skin. Since motion is under the direction of sensibility, organs of movement have much to do with the question. When perfection in this respect conflicts with perfection of brain, in evidence of position, we naturally give the preference to the latter in deciding. Thus the ruminating mammals are much superior to man in the structure of their feet, teeth and stomach, yet we properly assign the higher position to the quadrumana and to man, on account of the superior complication of their brain structure.

Palæontology has proven[1] what had been already surmised, that the development of animal organisms has been on lines of increasing specialization of parts. That is, in lines of increasingly perfect adaptations of structures to ends, or functions. In certain series of animals we witness steadily increasing perfection of mechanisms of the limbs for running; in others for digging; in others for flying. In the teeth we find increasing perfection of machines for grinding, for cutting or for seizing. In the brain the specialization has evidently been towards increased acuteness of perception, increased energy of action, and increased intelligence. Specialization does not, however, necessarily imply progressive development. Adaptation may be to a parasitic or a sessile mode of life. Such adaptation is often displayed in a very special modification of parts, as in the anterior limbs of some of the parasitic Crustacea; in the mouth parts of some Arachnida; in the feet of the sloth, and in the jaws of the ant-eaters.

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[1] Cfr. "On the Evidence for Evolution in the History of the Extinct Mammalia;" Proc. Amer. Assoc. Adv. Sciences for 1883.

Embryology has furnished, and will furnish, many important hints and demonstrations as to the true meaning of the rudimentary condition or absence of parts, and thus indicate the phylogenetic connections of animals. Thus the origin of the Tunicata from primitive vertebrate-like forms would probably never have been suspected but for embryological studies; and the origin of the very peculiar order of Rotifera has been explained in like manner. But embryology has its limitations, for the transitional characters presented by embryos are only partially of the nature of a record of the structures which belonged to their ancestors in successive geological ages, and are frequently special adaptations to the necessities of their embryonic life. Such are the statoblasts which are present in fresh-water sponges and Polyzoa, and wanting in the marine forms; and the allantois and placenta of Vertebrata. In a number of groups the embryo seems to have been more susceptible to the influence of the environment than the adults.[1] It results that in many cases the phylogeny can only be determined by the discovery and investigation of the ancestors themselves, as they are preserved in the crust of the earth. In all cases this discovery confirms and establishes such definite conclusions as may be derived from embryology. It is also clear that on the discovery of phylogenetic series it becomes at once possible to determine the nature of defective types. It becomes possible to ascertain whether their rudimental parts represent the beginnings of organs, or whether they are the result of a process of degeneration of organs once well developed.

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[1] A remarkable instance of this state of things appears in the history of the evolution of the insects. It is quite impossible to understand this history without believing that the larval and pupal states of the highest insects are the results of a process of degeneracy which has affected the middle periods of growth but not the mature results. The earliest insects are the Orthoptera, which have active aggressive larvæ and pupæ, undergoing the least changes in their metamorphosis (Ametabola) and never getting beyond the primitive mandibulate condition at the end. The metamorphosis of the jawed Neuroptera is little more marked, and they are one of the oldest orders.

The highest orders with jaws undergo a marked metamorphosis (Coleoptera, Hymenoptera), the Hymenoptera even requiring artificial intervention in some instances to make it successful. Finally the most specialized orders, the suctorial Diptera and Lepidoptera, especially the latter, present us with very unprotected more or less parasitic stages, both active and inactive. These animals have evidently degenerated, but not so as to prevent their completing a metamorphosis necessary for purposes of reproduction. As is well known, many imagines (Saturniidæ, Œstridæ) can perform no other function, and soon die, while in some Diptera the incomplete larvæ themselves reproduce, so that the metamorphosis is never completed.

This history is parallel to that proposed by Dohrn to account for the origin of the Ammocœtes larval stage of the Marsipobranchii. He supposes this form to be more degenerate than its probable ancestral type in the ancestral line of the Vertebrata, as it is inferior to its own adult. An inactive life in mud is supposed by Dohrn to have been the effective cause. An inactive life on the leaves of plants, or in dead carcases, has probably been the cause of the same phenomenon in the Lepidoptera and Diptera.

A great deal of light has been happily thrown on this question as regards the Vertebrata, by the recent work done in North American palæontology. The lines of descent of many of the minor groups have been positively determined, and the phylogenetic connections of most of the primary divisions or classes have been made out. The result of these investigations has been to prove that the evolution of the Vertebrata has proceeded not only on lines of acceleration but, to a much greater extent than has been heretofore suspected, on lines of retardation.[1] That is, that evolution has been not only progressive, but at times retrogressive. This is entirely in accord with the views derived by Dohrn from embryology,[2] who, however, wrote only of the origin of the Vertebrata as a whole and not of its divisions, excepting only the Leptocardii and Marsipobranchii, that is, of the sand lance and the lampreys and hags. The demonstration of such relations for the higher Vertebrata is now done nearly for the first time.[3]

Omitting from consideration the two classes above mentioned, whose remains have not yet been certainly found in a fossil state, there remain the following: the Pisces, Batrachia, Reptilia, Aves and Mammalia.

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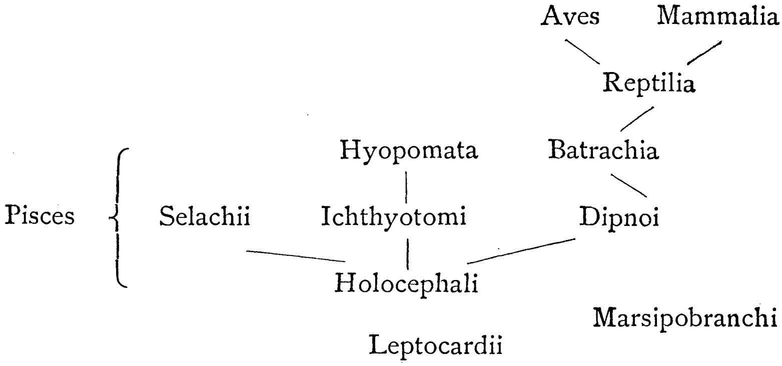
[1] See Origin of Genera, E. D. Cope, Philadelphia, 1868, where these terms are introduced.

[2] See Der Ursprung der Wirbelthiere u. d. Princip des Functionwechsels, Leipsic, 1875.

[3] On the Phylogeny of the Vertebrata, Cope, AMER. NATURALIST, Dec., 1884. I here remark that my researches have now, as I believe, disclosed the ancestry of the mammals, the bird, the reptiles and the true fishes, or Hyopomata, including the special phylogenies of the Batrachia and Reptilia, and some of the Mammalia. See the following references: AMERICAN NATURALIST, 1884, p. 1136; Proceedings Academy Philadelphia, 1867, p. 234; Proceedings American Philosoph. Society, 1884, p. 585; AMERICAN NATURALIST, 1884, p. 27; Proceedings American Association for the Advancement of Science, XIX, 1871, p. 233; Proceedings American Philosophical Society, 1882, p. 447; AMERICAN NATURALIST, 1884, pp. 261 and 1121; Report U. S. Geol. Survey W. of 100th Mer., G. M. Wheeler, 1877, IV, II, p. 282.

The Mammalia have been traced to the theromorphous reptiles by the Monotremata. The birds, some of them at least, appear to have been derived from the Dinosaurian reptiles. The reptiles in their primary representative order, the Theromorpha, have been probably derived from the rhachitomous Batrachia. The Batrachia have originated from the sub-class of fishes, the Dipnoi, though not from any known form. I have shown that the true fishes or Hyopomata have descended from an order of sharks,[1] the Ichthyotomi, which possess characters of the Dipnoi also. The origin of the sharks remains entirely obscure, as does also that of the Pisces as a whole. Dohrn believes the Marsipobranchii to have acquired its present characters by a process of degeneration. The origin of the Vertebrata is as yet entirely unknown, Kowalevsky deriving them from the Ascidians, and Semper from the Annelida. The above results I have embodied in the following phylogenetic diagram :



Accepting this phylogeny, it becomes possible to determine the course of development first of the whole series ; and secondly of the contents of each class taken by itself. I will first consider the direction of the evolution of the Vertebrata as a whole.

II. The Vertebrate Line.

The Vertebrata exhibit the most unmistakable gradation in the characters of the circulatory system.[2] It has long been the custom to define the classes by means of these characters, taken in connection with those of the skeleton. Commencing in the Leptocardii with the simple tube, we have two chambers in the Marsipobranchii and fishes; three in the Batrachia and Reptilia; and four in the Aves and Mammalia. The aorta-roots commence as numerous pairs of branchial arteries in the Leptocardii; we see seven in the Marsipobranchi, five in the fishes (with number reduced in some); four and three in Batrachia, where they generally cease to perform branchial functions; two and one on each side in Reptilia; the right hand one in birds, and the left hand one in Mammalia. This order is clearly an ascending one throughout. It consists of first, a transition from adaptation to an aquatic to an aërial respiration; and second, an increase in the power to aërate and distribute a circulating fluid of increased quantity, and of increased calorific capacity. In other words, the circulation passes from the cold to the hot-blooded type coincidentally with the changes of structure above enumerated. The accession of a capacity to maintain a fixed temperature while that of the surrounding medium changes, is an important advance in animal economy.

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[1] Proceedings Am. Phil. Soc., 1884, p. 585.

[2] See Origin of Genera, 1868, p. 20, for a table of the characters of the circulatory system.

The brain and nervous system also display a general progressive ascent. Leaving the brainless Leptocardii, the Marsipobranchs and fishes present us with small hemispheres, larger optic lobes and well-developed cerebellum. The hemispheres are really larger than they appear to be, as Rabl Rückard has shown[1] that the supposed hemispheres are only corpora striata. But the superior walls are membranous, and support on their internal side only a layer of epithelial cells, as in the embryos of other Vertebrata, instead of the gray substance. So that although we find that the cerebellum is really smaller in the Batrachia and most Reptilia than in the fishes, the better development of the hemispheres in the former gives them the preëminence. The Elasmobranchii show themselves superior to many of the fishes in the large size of their corpora restiformia and cerebellum. The Reptilia constitute an advance on the Batrachia. In the latter the optic thalami are, with some exceptions, of greater diameter than the hemispheres, while the reverse is generally true of the reptiles. The crocodiles display much superiority over the other reptiles in the larger cerebellum, with rudimental lateral lobes. The great development of the hemispheres in birds is well known, while the general superiority of the brain of the living Mammalia over all other vertebrates is admitted.

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[1] Biologisches centralblatt, 1884, p. 449

The consideration of the successive relations of the skeleton in the classes of vertebrates embraces, of course, only the characters which distinguish those classes. These are not numerous. They embrace the structure of the axis of the skull; of the ear bones; of the suspensors of the lower jaw; of the scapular arch and anterior limb, and of the pelvic arch and posterior limb. Other characters are numerous, but do not enter into consideration at this time.

The persistence of the primitive cartilage in any part of the skeleton is, embryologically speaking, a mark of inferiority. From a physiological or functional standpoint it has the same significance, since it is far less effective both for support and for movement than is the segmented osseous skeleton. That this is a prevalent condition of the lower Vertebrata is well known. The bony fishes and Batrachia have but little of the primitive cartilage remaining, and the quantity is still more reduced in the higher classes. Systematically then, the vertebrate series is in this respect an ascending one. The Leptocardii are membranous; the Marsipobranchii and most of the Elasmobranchii cartilaginous; the other Pisces and the Batrachia have the basicranial axis cartilaginous, so that it is not until the Reptilia are reached that we have osseous sphenoid and presphenoid bones, such as characterize the birds and mammals. The vertebral column follows more or less inexactly the history of the base of the skull, but its characters do not define the classes.

As regards the suspensor of the lower jaw the scale is in the main ascending. We witness a gradual change in the segmentation of the mandibular visceral arch of the skull, which clearly has for its object such a concentration of the parts as will produce the greatest effectiveness of the biting function. This is accomplished by reducing the number of the segments, so as to bring the resistence of the teeth nearer and nearer to the power, that is, the masseter and related muscles, and their base of attachment, the brain-case. This is seen in bony Vertebrates in the reduction of the segments between the lower jaw proper and the skull, from four to none. In the fishes we have the hyomandibular, the symplectic, the inferior quadrate, and the articular. In the Batrachia, reptiles and birds, we have the quadrate and articular only, while in the Mammalia, these elements also are wanting.

The examination of the pectoral and pelvic arches reveals a successive modification of the adaptation of the parts to the mechanical needs of the limbs. In this regard the air-breathing types display wide diversity from the gill-bearing types or fishes. In the latter, the lateral elements unite below without the intervention of a median element or sternum, while in the former the sternum or parts of it, are generally present. Either arrangement is susceptible of much mechanical strength, as witness the Siluroid fishes on the one hand, and the mole on the other. The numerous segments of the fishes' pectoral arch must, however, be an element of weakness, so that from a mechanical standpoint it must take the lowest place. The presence of sternal elements, with both clavicle, procoracoid, and coracoid bones on each side, gives the Reptilia the highest place for mechanical strength. The loss of the coracoid seen in the tailed Batrachia, and loss of coracoid and procoracoid in the Mammalia, constitute an element of weakness. The line is not then one of uniform ascent in this respect.

The absence of pelvis or its extremely rudimental condition in fishes, places them at the foot of the line in this respect. The forward extension of the ilium in some Batrachia and in the Mammalia, is to be compared with its backward direction in Reptilia, and its extension both ways in the birds. These conditions are all derived by descent from a strictly intermediate position in the Batrachia and Reptilia of the Permian epoch. The anterior direction must be regarded as having the mechanical advantage over the posterior direction, since it shortens the vertebral column and brings the posterior nearer to the anterior feet. The prevalence of the latter condition in the Mammalia enables them to stand clear of the ground, while the Reptilia move with the abdomen resting upon it. As regards the inferior arches of the pelvis, the Mammalia have the advantage again, in the strong bony median symphysis connecting the ischium and pubis.[1] This character, universal among the land Vertebrata of the Permian epoch, has been lost by the modern Batrachia, Reptilia, and birds, and is retained only by the Mammalia. So the line, excepting the Mam-

[1] This is an advantage as a protection during gestation.

malian, have *degenerated* in every direction in the characters of the pelvis.

The limbs of the Pisces are as well adapted to their environment as are those of the land Vertebrata, but from an embryological standpoint, their structure is inferior. The primitive rays are less modified in the fin than in the limb; and limbs themselves display a constantly increasing differentiation of parts, commencing with the Batrachia and ending with the Mammalia. The details of these modifications belong to the history of the contents of the classes however, rather than to the succession of the Vertebrata as a whole.

In review it may be said, that a comparison of the characters which define the classes of the Vertebrates, shows that this branch of the animal kingdom has made with the ages successive steps of progress from lower to higher conditions. This progress has not been without exception, since as regards the construction of the scapular arch, the Mammalia have retrograded from the reptilian standard, as a whole.

In subsequent articles I shall take up the lines of the classes separately.

(*To be continued.*)

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EDITORS' TABLE.

EDITORS: A. S. PACKARD AND E. D. COPE.

——The annual report for 1883–4 of Professor Agassiz to the president and fellows of Harvard College, on the condition of the Museum of Comparative Zoölogy, contains much matter of interest to the naturalist on the subject of the accumulation and care of collections. The director of the museum thinks that it is not advisable to create collections which "must undoubtedly be duplicated in Washington or New York." That portion which relates to the care of the perishable materials contains many suggestive statements. Among these is the information that the large collections of reptiles, fishes, mollusks, Crustacea and echinoderms in alcohol, made by the museum, have become in great degree useless for nice scientific work, and that every year much material has to be thrown away. Such a statement as this must be equally applicable to all museums. That it should be true is greatly to be regretted, and points clearly to the